

chromosomes small, probably  $x = 10$  (figs. 11, 12, 13), leaf epidermis with saddle-shaped siliceous cells and bicellular microhairs of the "ice cream cone" type (fig. 10), and leaf anatomy of the Kranz type (fig. 9). The statement of Sutton that the leaf anatomy is festucoid is certainly an error. Perhaps his material was from some festucoid grass mistakenly identified as *Redfieldia*. Since he cites no voucher specimens, this cannot be determined.

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## DEVELOPMENT OF MORPHOLOGICAL PATTERNS IN THREE SPECIES OF DELESSERIACEAE

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Small red algae with discrete, leaf-like blades borne on short stipes are inconspicuous, but not rare, in low intertidal and subtidal habitats. In California, such blades with distinct midribs and dentate margins are usually attributed to *Nienburgia andersoniana*, if they are polystromatic. If monostromatic, they are generally referred either to *Anisocladella pacifica* or to one of three species of *Phycodrys*, *P. isabellae*, *P. profunda*, or *P. setchellii* (Abbott and Hollenberg, in press).

The critical distinction between *Phycodrys* and *Anisocladella* is considered to be the way secondary cell rows form—symmetrically and equally on two sides of the central cell row in *Phycodrys* (Kylin, 1923) and unequally in *A. pacifica* (Kylin, 1941). Presumably, this early growth is related to the later development of lateral nerves, which are said to be opposite in *Phycodrys* and alternate or irregularly spaced in other genera where they are present (Smith, 1944; Taylor, 1945, 1957). In practice, however, when collections of *Anisocladella* and *Phycodrys* species are examined, nerves are absent or indistinct in some specimens of both genera. Therefore, venation is not a reliable character for separating such blades into distinct taxa.

Comparison of large numbers of field-collected specimens of *Phycodrys profunda*, *Anisocladella pacifica*, and *Nienburgia andersoniana* led me to think that characters other than blade morphology might be used to separate the taxa. Since very precise arrangements of cells in apices in these and related genera characterize taxa at several levels in the family (Kylin, 1956), it seemed reasonable to seek non-random development sequences that result in orderly arrangements of thallus parts. If existence of such patterns could be established by study of laboratory-grown thalli, characteristic morphologies might then be recognized in naturally occurring plants.

#### MATERIALS AND METHODS

Cultures of *Phycodrys profunda*, *Anisocladella pacifica*, and *Nienburgia andersoniana* were initiated from apices of freshly collected thalli and grown in 200 ml of an enriched natural seawater medium (Murray et al., 1972) without shaking. Two unialgal *Phycodrys profunda* cultures were maintained for more than a year through several cycles of the life-history and were cloned for experimental procedures. Apices of intertidal *Anisocladella pacifica* and *Nienburgia andersoniana* were snipped at several times during the study, dragged through agar, and exposed to GeO<sub>2</sub>. These cultures were grown for shorter periods of time and were seldom unialgal (see Chapman, 1973, for discussion of isolation and culture techniques). Sub-cultures were grown under several combinations of different light periods and intensities (250, 500, 1000 m-c; 8/16, 12/12, and 16/8 hrs. light/dark) and different temperatures (10°, 12°, 16° C). Not all combinations were used for all cultures. These conditions approximated ambient light and temperatures in or near the sites sampled. All cultures were transferred to new media at 3–6 week intervals during experimental periods. Thalli from numerous sites, to 30 m deep, in San Diego County were collected throughout the year; vouchers for all collections, including those that furnished culture inocula, are in the author's personal herbarium. Collections in herbaria elsewhere (AHFH, GMS, UC) were examined.

#### RESULTS

Early cell divisions: Cells close to primary apical cells in *Phycodrys*

*profunda* and *Anisocladella pacifica* are drawn in Figure 1. My observations of *Nienburgia andersoniana* apices agree with those of Nienburg (1908). In thalli of all three species, the central and pericentral cells, then the secondary and higher order cell rows, form in a similar way. The apical cells that first protrude from the margins are at different distances from the primary apical cell on the two sides of the blade apex, rather than being equidistant from the apex and opposite. These early dentations, and the nerves that appear later, tend to alternate in *Phycodrys profunda* and *Anisocladella pacifica*. Nerves are not formed in *Nienburgia* species.

As growth continues, however, development of structures from thallus margins is dissimilar in the three species. Laboratory-grown blades and axes are shown in Figures 2-4. These can be compared with field-collected plants in Figures 5-7.

*Phycodrys profunda*: On cultured thalli, haptera (fig. 2 a) form directly from marginal cells of the blades and commonly terminate in uniseriate, multicellular rhizoids (fig. 2 b). Before rhizoids form, the haptera appear as smooth-tipped, tapered, terete spines (fig. 2 d). Haptera and rhizoids form without direct contact between the thallus and culture dish surfaces. A narrow blade occasionally grows from the side

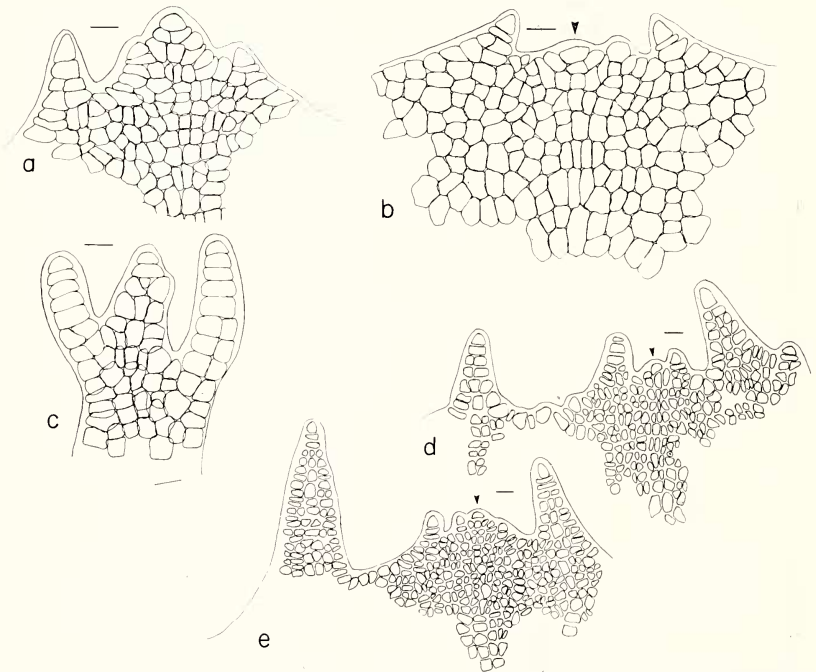
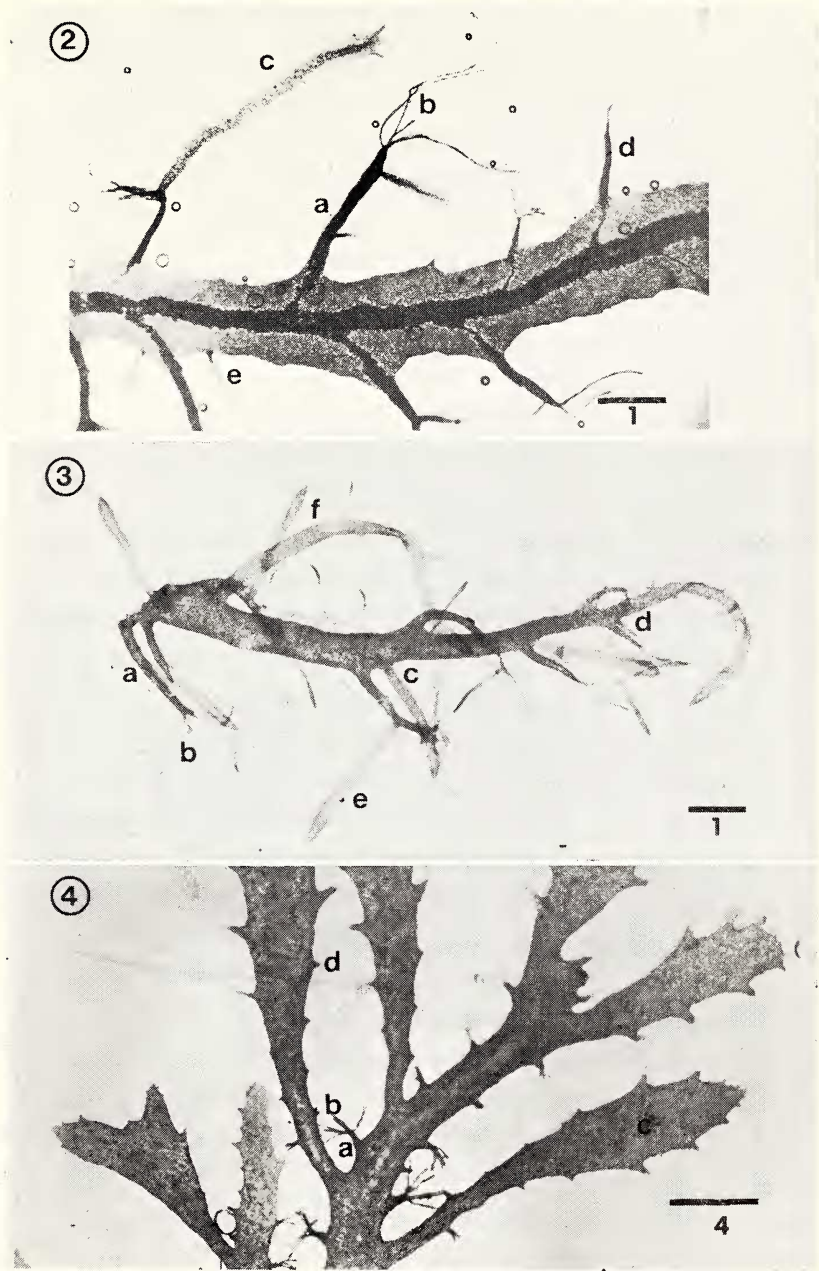


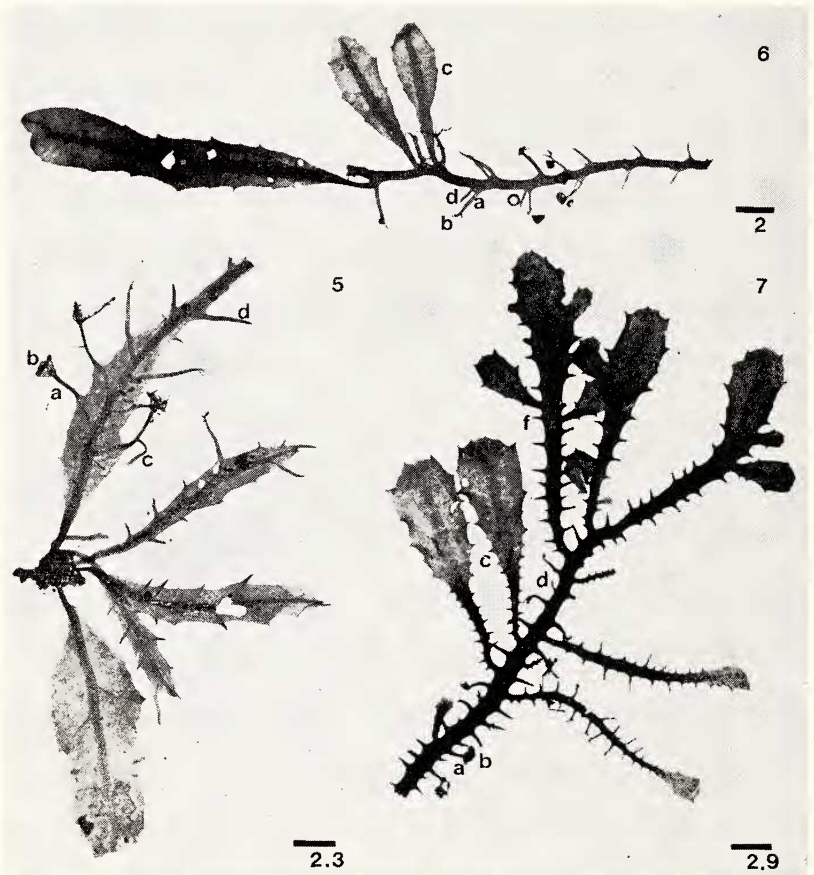
FIG. 1. Arrangement of cells near primary apical cell in *Anisocladella pacifica* (A-C) and *Phycodrys profunda* (D-E). A,B,D, and E, blades. C, prostrate axis. Scale = 15  $\mu$ m; Arrows = primary apical cells.



FIGS. 2-4. Laboratory-grown thalli of algae. 2, *Phycodrys profunda*. 3, *Anisocladella pacifica*. 4, *Nienburgia andersoniana*. Scales are in mm; a = hapteron, b = rhizoids, c = secondary blade, d = spine, e = adventitious blade, f = branch axis.

(fig. 2 c) of an older hapteron after terminal rhizoids have formed. These secondary blades develop midribs, nerves, and marginal haptera in the same manner as do primary blades. Secondary blades do not grow directly from margins of primary blades during this initial growth period. On some older thalli, very narrow blades are initiated adventitiously from blade margins (fig. 2 e) in positions apparently unrelated to structures already present. These bladelets remain small and unbranched.

Haptera and secondary blades are borne in the same way on field-collected thalli. Tips of haptera (fig. 5 a), fastened by rhizoids (fig. 5 b) to a substrate, become torn when the plant is removed. Lateral blades on haptera are rare (fig. 5 c). Reproductive structures that correspond to those on the primary blade can occur on secondary blades. Secondary



FIGS. 5-7 Field-collected thalli of algae. 5, *Phycodryis profunda*. 6, *Anisocladella pacifica*. 7, *Nienburgia andersoniana*. Scales are in mm; a-f as in Figures 2-4.

blades do not occur directly on margins of other blades. Primary blades are subtended by short terete stipes that branch from other stipes or grow from small, discrete holdfasts. Nerves are more often alternate than opposite, but their arrangement varies. No prostrate axes were found. Haptera can develop from the point on the margin where a nerve terminates, but often the positions of the two are unrelated. On many specimens the marginal projections are undifferentiated, appearing as short dentations or spines (fig. 5 d).

*Anisocladella pacifica*: Width of blades varied in cultured thalli. I was often uncertain whether to interpret a given region as blade or axis. After forming narrow thallus parts for several weeks, an apex may produce an expanded, more blade-like part. Photographic records of individual thalli show that haptera with rhizoids (fig. 3 b) develop first in positions that alternate on opposing sides. Very small spines (fig. 3 d), or narrow dentations, form very close and just distal to haptera. These later grow out to become secondary blades (fig. 3 c), or they may remain narrow as they branch and function as axes (fig. 3 f). Very rarely, blades grow from lateral positions on haptera (fig. 3 e).

On axes of field-collected thalli (fig. 6), haptera and erect blades (or axial branches) are in pairs in a definite pattern, or one or both of the structures may be an undifferentiated spine. Where both structures are developed, the hapteron is always proximal and the blade distal. These pairs grow from opposite edges of erect and prostrate axes in an alternate arrangement. All axes terminate in blades. On axes appressed to substrates, haptera (fig. 6 a) are fastened to the substrate, presumably by means of terminal rhizoids (fig. 6 b), and the adjacent structure is a simple spine (fig. 6 d). Where the axis bears blades (fig. 6 c) or other axes, a spine in a proximal position represents the incipient hapteron. Blade margins typically are dentate. The extent to which nerves are developed and arrangement of nerves vary.

*Nienburgia andersoniana*: On laboratory-grown thalli, haptera and secondary blades develop on margins of both prostrate axes and erect blades. Regularly spaced haptera with rhizoids (fig. 4 a,b) develop alternately on one then on the other edge before blades (fig. 4 c) appear in between the haptera.

Plants collected in the field (fig. 7) exhibit the same alternate arrangements of marginal structures on all thallus parts. Spines frequently occur in place of either haptera or blades. A branch axis can replace a blade anywhere on the thallus.

Reliability of patterns: These patterns in the way blades and haptera are arranged in each taxon were a reliable way to distinguish the three species, although on some damaged thalli they are difficult to recognize. Each of the patterns proved to be species-specific, and their development was unaffected by different regimes of light and temperature when thalli were grown in the laboratory.

## DISCUSSION

In *Phycodrys profunda*, early development of cell rows and, later, the irregular formation of nerves, resemble comparable stages in the *Nienburgia* and *Anisocladella* species and do not distinguish thalli of one species from another. These two aspects of growth, and the positions of marginal dentations, are asymmetrical on the two edges of the blades. For *Nienburgia andersoniana* and *Anisocladella pacifica* apices, these observations agree with earlier descriptions of these species (Nienburg, 1908; Kylin, 1941) but disagree in respect to the characterization presently accepted for *Phycodrys* species (Kylin, 1956).

Kylin considered that the symmetrical development he ascribed to *Phycodrys sinuosa* (Kylin, 1923) was significantly different from that of *Anisocladella*, *Nienburgia*, and other genera in the same group. Since *P. sinuosa* (= *P. rubens*: see discussion of nomenclature in Dixon, 1964) is the type species, this characterization has been extended to other species of the genus (Kylin, 1956). Rosenvinge (1931) stated, in support of Kylin's study, (since) "the two initial segments of a segment always behave in the same manner, the lobes are always opposed". Writers of various algal floras (see above) mention opposite nerves in describing the genus, perhaps following the opinion of Kylin rather than as a result of critical evaluation of the character.

*Phycodrys rubens* on both sides of the north Atlantic is a rather common species and *P. setchellii* in the Pacific is very similar. In both, nerves are often strikingly and regularly opposite, but thalli of each species can be found in which the arrangement of nerves varies in the same ways as described here for specimens of *P. profunda*. Dawson (1962) did not mention apical anatomy in *P. profunda* but he did refer to "opposite veins". *Phycodrys isabellae* nerves were said to be opposite but often weakly developed or lacking (Norris and Wynne, 1968). Many other species attributed to the genus are seldom collected and known only from scant material. Arrangements of nerves other than precisely or even approximately opposite are associated with certain of these. Taylor (1945) stated that *P. elegans* (as *P. pulchra*) possesses "irregularly alternate lateral veins". Nerves of *P. amplissima* are arranged very irregularly (Dawson, 1962). Wynne (1970) characterized *Phycodrys* blades in general as being "heavily veined" but he did not use "opposite" in this context. It may be that the criteria of equally developed, opposite secondary cell rows and the perhaps concomitant development of symmetrical nerves cannot be strictly applied to any species of *Phycodrys* when numerous collections are studied. The proportion of bilaterally symmetrical blades certainly varies between, as well as within, species. The secondary cell rows on opposite sides of the midrib are frequently unequal in *P. profunda*; since one of the two lateral pericentral cells in each segment is always formed before the other, the two apical cells of opposing cell rows form at different times, and it seems reasonable that this inequality might persist in subsequent development.

Marginal haptera on blades, such as characterize *P. profunda*, are found infrequently on *P. setchellii*. On blade margins of *P. isabellae*, there are "terete rhizoid-bearing processes that may form secondary attachments" (Norris and Wynne, 1968). Similar structures occur on blades of *P. lucasana* (Dawson, 1962). Lateral blades, from the sides of haptera, are rarely seen, but evidently the potential for their development exists in *P. profunda* and *P. setchellii* at least. Specimens of many species of *Phycodrys* have numerous secondary bladelets borne directly on margins of larger blades. Most of these species are larger than *P. profunda* so blade margins would be less likely to be in contact with substrate surfaces to which haptera might attach. Descriptions of these species do not mention prostrate axes. The absence of regularly branched prostrate axes possibly can be shown to demarcate *Phycodrys* species from species of other genera with haptera and blades arranged in orderly ways on prostrate axes.

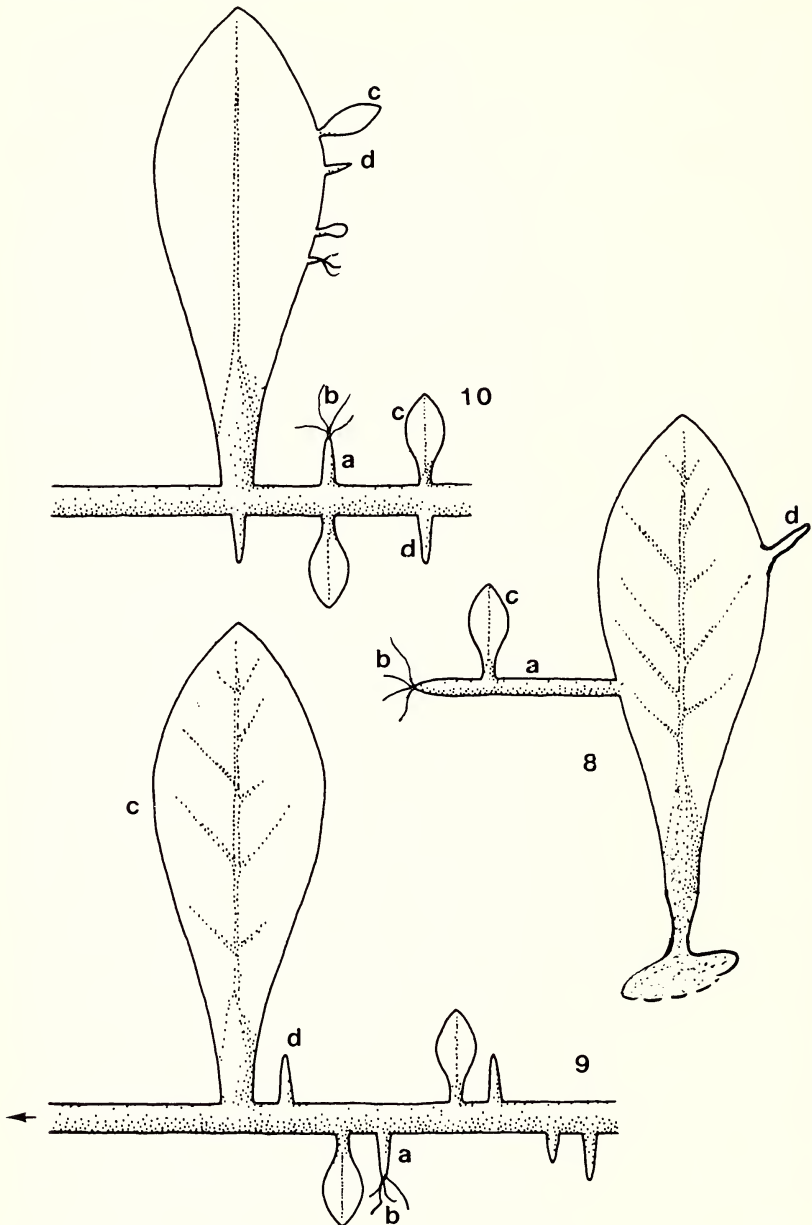
Use of the patterns described here as distinguishing three species (cf. figs. 8-10) might be extended to the generic level. Although limited, available information supports use of the patterns for *Nienburgia* and *Anisocladella*. The only parts of *A. serratodentata* (the type and only other species of *Anisocladella* known) that have been described are dentate blades (Skottsberg, 1923; Kylin, 1956; as *Delesseria serratodentata*, Kylin and Skottsberg, 1919). In discussing *Nienburgia prolifera*, Wynne (1970) definitely alludes to an arrangement of parts such as shown here for *N. andersoniana* (fig. 10). Descriptions of species from South Africa (*Nienburgia serrata*, Papenfuss, 1956, as *Nitophyllum serratum* in Suhr, 1836; *Nienburgia pinnatifida*, Papenfuss, 1968, as *Nitophyllum pinnatifidum* in Suhr, 1834) do not mention prostrate axes or haptera. European species are not known (P. S. Dixon, pers. comm.). Thus, there are no species in either genus that can be shown to lack the patterns described here or to have different arrangements of branches.

The development described in the three species studied here can be interpreted in terms of two kinds of branches that are formed in regular sequences. A hapteron that ceases to elongate when terminal rhizoids form is a determinate branch. It does not repeat its own development to form new haptera. Blades are equivalent to axes insofar as both are indeterminate branches that are capable of unlimited growth behind a persistent primary apical cell. These branches repeat the developmental sequences by which they were formed. Certain marginal cells on indeterminate branches (blades and axes) can become apical cells of either determinate or indeterminate branches; determinate branches form only lateral indeterminate branches. The two types of branches form in predictable sequences while the thallus is growing and their final arrangement is orderly and distinctive in each species.

Other observations suggest that different apical cells on margins have different potentials for rates and orientation of cell division. As far behind the apex as cell rows can be traced clearly, neither rows of higher order than secondary nor accessory rows derived from intercalary cells



of the central cell row grow beyond the margins. The potential to convert to growth as primary apical cells may be restricted to apical cells of sec-



FIGS. 8-10. Diagrams of branching patterns in algae. 8, *Phycodrys profunda*. 9, *Anisocladella pacifica*. 10, *Nienburgia andersoniana*. Arrow indicates direction of apex; a-f as in Figures 2-4.

ondary cell rows. The space between adjacent marginal dentations increases with distance behind the apex, corresponding to the development of other rows of cells between secondary cell rows. In these genera, only cells of secondary cell rows divide perpendicularly to the plane of the blade to produce thickened nerves. The regular spacing of determinate and indeterminate branches along prostrate axes in *Anisocladella pacifica* and *Nienburgia anderssoniana* and the tendency of haptera to be aligned with nerves in *Phycodrys profunda* support the conclusion that differentiation of marginal apical cells is rather precisely regulated.

Marginal branching patterns have proved to be reliable for recognition of the three species studied here. Apart from the taxonomic usefulness, the distinctions also imply that regulation of morphogenesis extends to regions of the thallus far removed from the primary apex and persists throughout the growth of the thallus.

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ARMILLARIA (TRICHOLOMATACEAE, AGARICALES)  
IN THE WESTERN UNITED STATES INCLUDING  
A NEW SPECIES FROM CALIFORNIA

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*Armillaria* Kummer has, to a large extent, been neglected by agaricologists, and no extensive treatment of North American species has appeared since that of Kauffman (1922). Prior to his publication, the only available treatment of the genus was that of Murrill (1914). Both of these works are difficult to use because many species that no longer belong in *Armillaria* are included. The common occurrence of a new species, described below, as well as the frustration resulting from the inability to identify numerous collections belonging to this genus, stimulated us to devote some time to the taxonomy of the species that occur in California, and, to a lesser extent, to those occurring in western United States. Results of this investigation along with a key to western North American *Armillarias* are presented below. Colors in quotations are from Ridgway (1912).

*Armillaria*, as conceived by us, includes those white-spored mushrooms that have attached rather than free lamellae, a centrally attached stipe, and a partial veil that usually forms an annulus. Based on their frequency of appearance, two groups of *Armillaria* species can be recognized in the United States west of the Rocky Mountains. One group, which includes *A. mellea*, *A. ponderosa*, *A. zelleri*, *A. albolanaripes*, and *A. olida*, fruits every year and usually in considerable abundance. The second group contains species that appear only sporadically and are rare, particularly in California. Included in this group are *A. caligata*, *A. subcaligata*, *A. robusta*, *A. luteovirens*, and *A. viscidipes*.